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Co-occurring Cuban dwarf boas (*Tropidophis*) show limited dietary differentiation

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Abstract

Interspecific and intraspecific niche partitioning have been widely documented in sympatric snakes. Size variation and ecological differentiation in co-occurring *Tropidophis* in Cuba suggest differences in diet. We compared dietary composition and niche breadth among three species of *Tropidophis* in central Cuba: *T. pardalis* (n = 13), *T. semicinctus* (n = 28), and *T. melanurus* (n = 86; 80 large, 6 small individuals). We found complete overlap in diet composition among *T. pardalis*, *T. semicinctus*, and small *T. melanurus*, all of which specialized on lizards of the genus *Anolis*. In contrast, large *T. melanurus* had a distinct diet, consisting mostly of amphibians (95%), particularly the Cuban treefrog (*Osteopilus septentrionalis*; ca. 70%) and two species of toads of the genus *Peltophryne* (ca. 26%), suggesting an ontogenetic shift in the diet of *T. melanurus*. The three species of *Tropidophis* had a narrow trophic niche ($B' \leq 0.280$).

Key Words

competition, dietary overlap, ecological segregation, generalist, specialist, snake assemblage, West Indies

Introduction

Competition, which negatively affects at least one interacting party (Begon et al. 2006), often drives sympatric species and different classes within a species to reduce overlap through ecological segregation (Gause 1934; Hutchinson 1957; Schoener 1971, 1974, 1982; Polis 1984; Tokeshi 1999). Food is one of the most obvious limiting resources that may drive competition in animals. In snakes, suitable prey may be probabilistically scarcer than in non-gape-limited predators (Greene 1983, 2001; Shine 1991; Forsman 1996; Rodríguez-Robles et al. 1999). Snakes may segregate ecologically by activity, habitat, temperature, or diet – with food availability often driving size- and morphology-based dietary adaptations (Greene 1983; Toft 1985; Reinert 1993; Luiselli 2006; Greene 2001; Luiselli et al. 2015; Hampton 2014; Lillywhite 2014). Such adaptations allow species and classes within to use specific resources more efficiently than congeneric relatives (e.g., Lillywhite and Henderson 1993; Lillywhite 2014). Snakes are well suited to study interspecific competition and resource partitioning (e.g., Shine and Bonnet 2000; Luiselli 2006). Both trophic niche partitioning and diet overlap in sympatric snakes have been widely documented (e.g., Toft 1985; Fitch 1999; Luiselli 2006; Pizzatto et al. 2009; Di Pietro et al. 2020), including intraspecific niche partitioning (e.g., Lind and Welsh 1994; Pearson et al. 2002; Perkins et al. 2020).

Despite extensive research on dietary niche partitioning in snakes, one group remains largely unstudied: the Neotropical genus *Tropidophis* Bibron, 1843 (Tropidophiidae). These are relatively small – usually < 1,000 mm snout–vent length (SVL) – mainly nocturnal, constricting, viviparous snakes (Hedges 2002; Henderson and Powell 2009; Franco Curcio et al. 2012; Rodríguez-Cabrera et al. 2021a). This genus comprises 33

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species from South America and the West Indies, with 17 endemic to Cuba (Hedges 2002; Henderson and Powell 2009; Franco Curcio et al. 2012; Torres López et al. 2017; Powell and Henderson 2012; Uetz et al. 2022; Zaher et al. 2024). Cuba is the only territory where several species of *Tropidophis* co-occur, with evident morphological and behavioral differentiation between them (Hedges and Garrido 1992; Hedges 2002; Rodríguez-Cabrera et al. 2020a, 2021a, 2021b; Zaher et al. 2024). Rodríguez-Cabrera et al. (2016) first proposed that the ecotypes observed in Cuban *Tropidophis* may reflect diet specialization within this group. Although we are not testing the ecotypes hypothesis here, we have compiled sufficient dietary data to test for inter- and intraspecific dietary segregation in a *Tropidophis* assemblage whose members – *T. melanurus* (Schlegel, 1837), *T. semicinctus* (Gundlach and W. Peters, 1865), and *T. pardalis* (Gundlach, 1840) – co-occur throughout Cuba and show phenotypic and ecological differentiation. *Tropidophis melanurus*, the largest species in the genus (> 1,000 mm SVL), is an ecological generalist with a varied diet including birds, mammals, amphibians, and reptiles (Rodríguez-Cabrera 2018; Rodríguez-Cabrera et al. 2016, 2020a, 2020b, 2021a, 2021b, 2022). *Tropidophis semicinctus* is medium-sized (408 mm SVL), gracile, semi-arboreal, and preys on anole lizards (Rodríguez-Cabrera et al. 2020a). *Tropidophis pardalis* is small (287 mm SVL), stout, ground-dwelling, and feeds on frogs and lizards (Armas and Iturriaga 2017; Rodríguez-Cabrera et al. 2020a, 2020b; Rodríguez-Cabrera and Hernández Gómez 2021). As these species differ in body size and shape, we tested the hypothesis that diet composition differs between these three species.

Just as differences in morphology and ecology can promote dietary segregation among species, variation within species – particularly across developmental stages – can also lead to niche partitioning. In snakes, ontogenetic dietary shifts are common and typically driven by changes in body size and gape limitation, which constrain the range of prey that individuals can capture and consume (Greene 1983, 2001; Shine 1991; Arnold 1993; Forsman 1996; Cochran et al. 2021; Patterson et al. 2022). Among our target species, *T. melanurus* stands out for its pronounced size disparity between neonates (~230 mm SVL, ~4 g; authors unpubl. data) and adults (> 1,000 mm SVL and > 800 g; Rodríguez-Cabrera et al. 2021a). This substantial size difference suggests the potential for shifts in dietary composition across life stages. We therefore tested the hypothesis that small and large *T. melanurus* differ in diet, indicating ontogenetic niche partitioning within this species.

The available information on the diet of these three species suggests that *T. pardalis* and *T. semicinctus* consume only a few prey types, whereas *T. melanurus* is more generalist (Henderson and Powell 2009; Franco Curcio et al. 2012; Fong et al. 2013; Rodríguez-Cabrera et al. 2020a, 2020b, 2021b, 2022; Rodríguez-Cabrera and Hernández Gómez 2021). Different levels of trophic specialization could be expected in sympatric species of *Tropidophis* with such strong differences in size and body shape. Thus, we tested the hypothesis that *T. pardalis* and *T. semicinctus* are trophic specialists, whereas *T. melanurus* is a trophic generalist. Accordingly, we predicted that the first two species would exhibit narrower dietary niche breadths than *T. melanurus*.

Methods

Study area

We collected data from 12 localities no more than 25 km apart between the two most distant, all situated around Santa Clara City, Villa Clara Province (Fig. 1; Appendix 1). This area of 258 km² is primarily covered by dry lowland xeromorph serpentine shrub woods, also known as "cuabal" (Borhidi 1991), with various degrees of disturbance including almost complete replacement by secondary vegetation (pastures, eucalyptus plantations, groves, invasive thorny scrublands), crops, and urban or suburban habitats (Fig. 2). Throughout, open vegetation predominates, with an abundance of serpentine rocks (Fig. 2), which are frequently used as shelter by snakes. The localities ranged between 80 and 150 m in elevation. To avoid potential seasonal bias, we sampled mostly during the rainy season, when vertebrate activity typically peaks.

Data collection

Some of the data used here were published in previous contributions (Rodríguez-Cabrera et al. 2020b, 2021b; Table 1). We collected the dietary information directly in the field over a span of about 40 years (1980–2021), from snakes either observed preying or found with stomach contents. In snakes with visible bulges in the stomach, indicating a recent meal, we forced regurgitation by palpation (Luiselli and Amori 2016). We identified each prey item to the lowest taxonomic level possible. Most feeding events recorded were incidental to other work, so an accurate measurement of the snakes was not always possible; hence, we visually estimated the snake's total length (TL). For *T. melanurus*, we grouped individuals into two size classes: small (≤ 350 mm TL, corresponding to individuals less than a year old; authors, unpubl. data) and large (> 350 mm TL). Because we found no juvenile *T. pardalis* and only one juvenile *T. semicinctus* (Fig. 3), we did not divide them by size.

Hypothesis testing

To test the research hypotheses of differences in diet among co-occurring *Tropidophis* and of ontogenetic shift in diet in *T. melanurus*, we compared prey type frequency. We tested the statistical null hypothesis of no association between prey type frequency and *Tropidophis* species/size class. We classified the prey items as "amphibian"

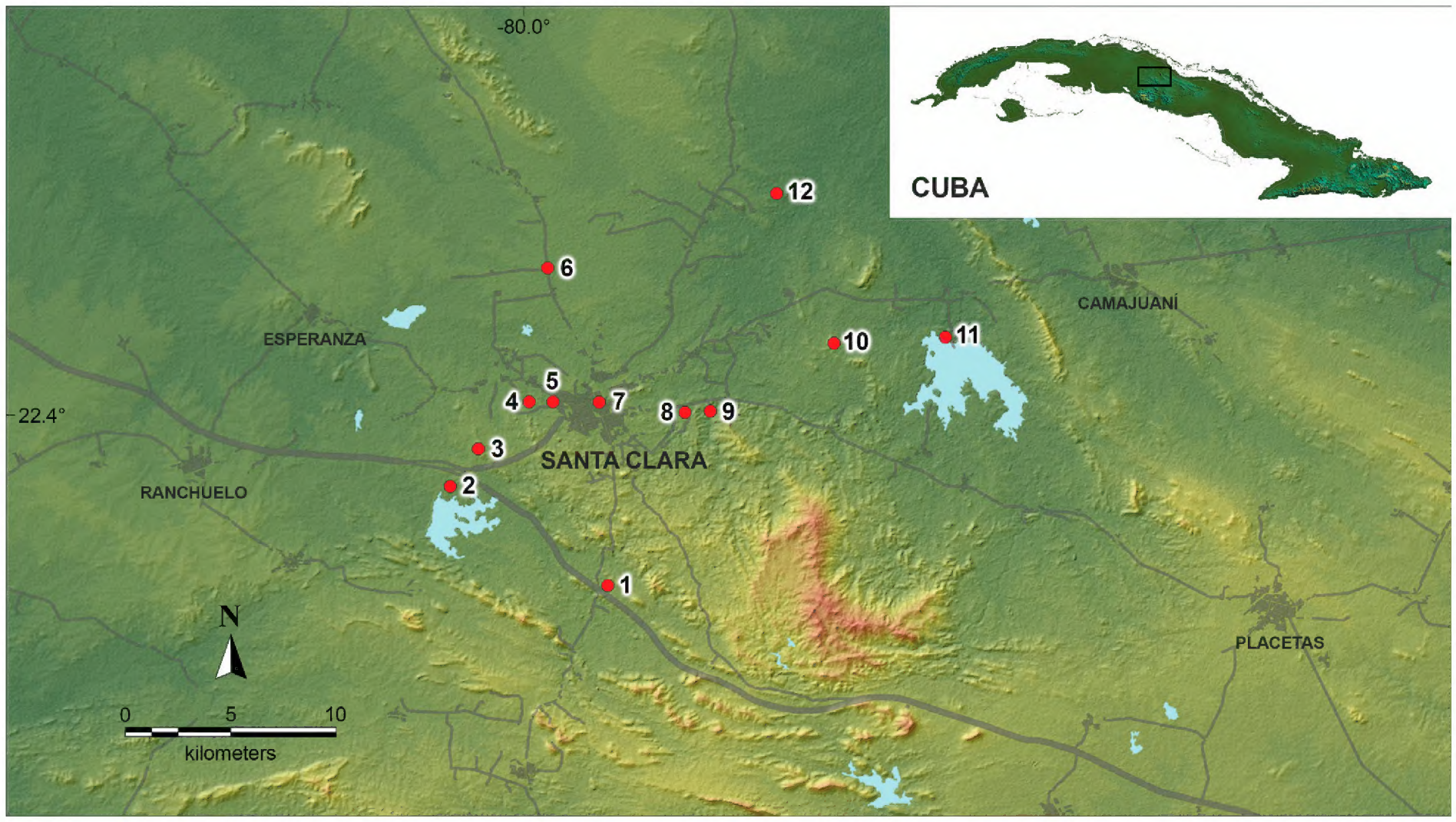

Figure 1. Map of central Cuba depicting the 12 localities around Santa Clara City, Villa Clara Province, where we collected dietary data from three sympatric species of *Tropidophis* (see Appendix 1). Gray lines and shading depict roads and urban areas, respectively.

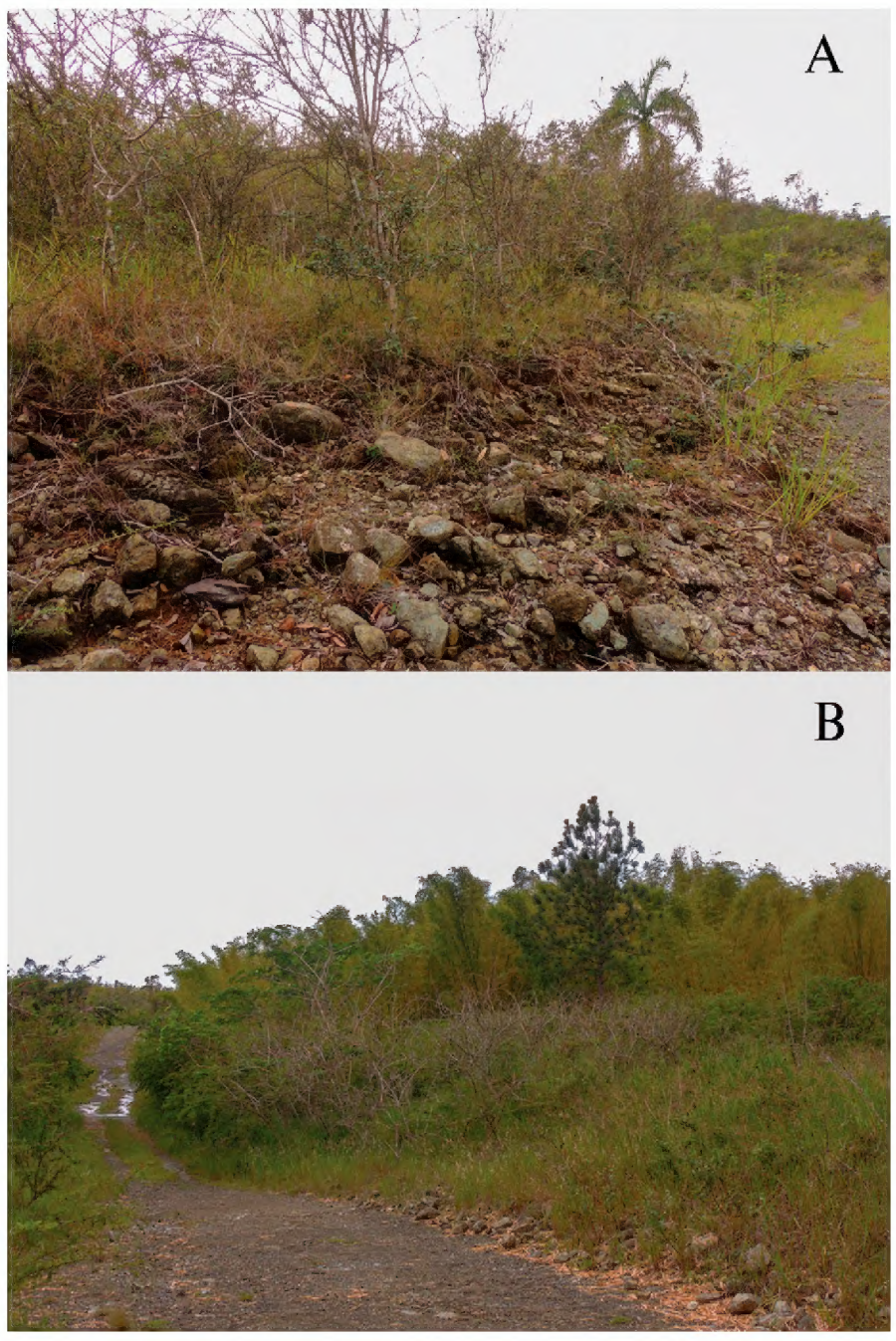

Figure 2. Main habitat types in the study area around Santa Clara City, Villa Clara Province, Cuba: dry lowland xeromorph serpentine shrubwood, also known as "cuabal" (**A**), and secondary vegetation (**B**). Photographs by T.M. Rodríguez-Cabrera.

or "lizard" and discarded mammals and birds because they occurred in the diet of only one category (large *T. melanurus*) and in low relative frequency (3.75% and 1.25%, respectively). We recorded prey type frequency per *Tropidophis* species/size class and made four contingency tables with prey types vs. *T. pardalis* and *T. melanurus* (1), *T. semicinctus* and *T. melanurus* (2), small *T. melanurus* and large *T. melanurus* (3), and *T. pardalis*, *T. semicinctus* and small *T. melanurus* (4). We tested the null hypotheses by conducting Fisher's exact test or Pearson's chi-square test according to the presence or absence of expected values smaller than 5, respectively. We used the functions "fisher.test" and "chisq.test" from the core package "stats" in the statistical software R v. 3.6.2 (R Core Team 2019).

To test the hypothesis of different levels of trophic specialization in the three species of *Tropidophis* and size categories within *T. melanurus*, we estimated trophic niche breadth (Krebs 1998) using the standardized version of Levins' (1968) niche breadth (Hurlbert 1978): $B' = (B-1)/(n-1)$, and $B = \sum p_j^2$, where B' is the standardized version of Levins' niche breadth, B is Levins' measure of niche breadth, n is the number of possible resource states, and p_j is the proportion of individuals found using resource state j. Levins' standardized niche breadth ranges from 0 to 1. A value of 1 is reached when all resource states are used equally across individuals, indicating a broad niche and low specialization. A value of 0 occurs when only one resource state is used by all individuals, reflecting a narrow niche and high specialization.

To test for differences in diet specialization between *T. pardalis* and *T. semicinctus* compared with

T. melanurus, we included all dietary cases to represent as much diversity in the diet as our sample size allowed and conducted niche breadth analyses. To this end, we generated two datasets. In one dataset, we grouped the prey by class – i.e., amphibians (*Eleutherodactylus*, *Osteopilus*, and *Peltophryne*), reptiles (*Anolis*), birds (Passeriformes), and mammals (*Mus* and *Rattus*) – to test for differences at the class level (Table 1). Then, to test for differences in diet at the highest possible taxonomic resolution and by body size, shape, and skin texture, we assembled a second dataset with lizard, bird, and mammal categories, and split amphibians into two – frogs (*Osteopilus* and *Eleutherodactylus*) and toads (*Peltophryne*) – because of differences in size, ecology, skin texture, and anti-predation mechanisms (Henderson and Powell 2009).

Results

General diet composition and feeding behavior

We analyzed dietary data from 127 individual snakes: *T. pardalis* (n = 13), *T. semicinctus* (n = 28), and *T. melanurus* (n = 86; 80 large, 6 small individuals). Each snake had consumed a single prey item. The three species consumed almost exclusively ectotherms over endotherms, *T. melanurus* being the only species to very occasionally include mammals and birds in its diet (3.49% and 1.16%, respectively) (Table 1).

Only eight *T. melanurus* and one *T. semicinctus* were constricting or swallowing their prey when detected; the rest were inactive snakes with stomach contents. The predation events by *T. melanurus* included a small individual preying upon a Five-striped Grass Anole (*A. ophiolepis*), a very large individual (ca. 1,000 mm TL) preying upon an Eastern Giant Toad (*P. peltocephala*), and six large individuals (> 600 mm TL) preying upon Cuban treefrogs (*O. septentrionalis*) (Fig. 3). Predation events were observed at night, except for three cases. A *T. semicinctus* was swallowing a Cuban Brown Anole (*A. sagrei*) under a rock that we turned over at 09:42 h (Fig. 3). The very large *T. melanurus* preying upon the *P. peltocephala* was first seen constricting its prey around 07:00 h and finished swallowing around 13:00 h. We observed another large *T. melanurus* swallowing an adult *O. septentrionalis* early in the morning. In the latter two cases, the snakes apparently captured their prey before dawn.

Diet differentiation

The proportion of amphibians and lizards consumed differed significantly between *T. pardalis* and *T. melanurus* ($P < 0.001$), between *T. semicinctus* and *T. melanurus* ($P < 0.001$), and between small and large *T. melanurus* ($P < 0.001$; Table 2). Thus, the research hypothesis of differ-

Table 1. Prey items consumed by *Tropidophis* species/categories. In all cases, there was a single prey item per snake. Large *T. melanurus* consumed 68.75% frogs, 26.25% toads, 3.75% mammals, and 1.25% birds. The remaining categories consumed anoles only.

Snake category	Prey	No. items	Source
T. pardalis	*Anolis ophiolepis*	2	This paper
	Anolis sagrei	11	This paper
T. semicinctus	*Anolis ophiolepis*	1	This paper
	Anolis sagrei	26	This paper
	Anolis sp.	1	This paper
T. melanurus (small)	*Anolis ophiolepis*	1	This paper
	Anolis sagrei	5	This paper
T. melanurus (large)	*Eleutherodactylus* sp.	1	Rodríguez-Cabrera et al. 2020b
	Osteopilus septentrionalis	54	This paper
	Peltophryne taladai	3	This paper
	Peltophryne peltocephala	18	This paper
	Unidentified bird (Passeriformes)	1	This paper
	Mus musculus	2	Rodríguez-Cabrera et al. 2021b
	Rattus rattus	1	Rodríguez-Cabrera et al. 2021b

Table 2. Fisher's exact test or Pearson's chi-square (χ^2) results for amphibian and lizard frequency versus *Tropidophis* categories. Fisher's exact test does not report a test statistic or degrees of freedom (DF); hence the NAs.

Category	χ^2 (DF, N)	P-value
T. pardalis and *T. melanurus*	NA (NA, 95)	7.775×10^{-12}
T. semicinctus and *T. melanurus*	79.676 (1, 110)	2.2×10^{-16}
small *T. melanurus* and large *T. melanurus*	NA (NA, 82)	2.856×10^{-9}
T. pardalis, *T. semicinctus*, and small *T. melanurus*	NA (NA, 47)	1

Figure 3. Individuals of the three species of *Tropidophis* studied in the surroundings of Santa Clara City, Villa Clara Province, Cuba: adult *T. pardalis* (**A**); juvenile *T. semicinctus* found swallowing a Cuban brown anole (*Anolis sagrei*) during the day (**B**); and adult *T. melanurus* constricting a Cuban treefrog (*Osteopilus septentrionalis*) (**C**), the prey item most frequently consumed by large individuals of this species. Photographs by T.M. Rodríguez-Cabrera (**A**), E. Morell Savall (**B**), and R. López-Silvero (**C**).

ence in diet between those categories is supported. On the contrary, there were no statistically significant differences in the prey types consumed between *T. pardalis*, *T. semicinctus*, and small *T. melanurus* ($P = 1$; Table 2).

Trophic niche breadth and overlap

Three categories showed the lowest possible Levin's niche breadth index ($B' = 0$): *T. pardalis*, *T. semicinctus*, and small *T. melanurus*. These groups consumed exclusively lizards of the genus *Anolis* (*A. ophiolepis* and *A. sagrei*), showing a complete overlap in their diets (Table 1).

Large *T. melanurus* had a slightly more varied dietary composition, but when we calculated Levins' niche breadth index for three resource states (amphibians, birds, and mammals), it increased only slightly ($B' = 0.053$). When Levins' niche breadth index was calculated for four resource states (frogs, toads, birds, and mammals), it increased more ($B' = 0.280$). When we analyzed *T. melanurus* as a species, including both small and large individuals into a single category, and considering all five resource states (frogs, toads, lizards, birds, and mammals), it showed a similar value of Levins' niche breadth ($B' = 0.276$) as large *T. melanurus* with four resource states. Amphibians made up 95% of the diet of large *T. melanurus*, with *O. septentrionalis* comprising nearly 70% of those (Table 1). Toads of the genus *Peltophryne* were consumed only by large *T. melanurus* exceeding 600 mm TL and represented over 26% of the diet of this category (Table 1).

Discussion

Resource use partitioning is the primary mechanism that drives competition avoidance and allows stable coexistence of species in natural ecosystems (e.g., MacArthur and Levins 1967; Schoener 1971, 1974, 1982). Our findings support both dietary differences and overlap in the studied *Tropidophis* assemblage.

The high overlap in the diets of *T. pardalis*, *T. semicinctus*, and small *T. melanurus* suggests a high interference competition among these categories. However, this apparent contradiction of the competitive exclusion principle (Gause 1934) could be explained by ecological segregation in axes other than the trophic niche. The different body plans of these species suggest that such ecological segregation might occur along the spatial niche axis. Some body plans can be used as proxies to predict habitat use in snakes. Specifically, stocky snakes with circular transverse sections are associated with terrestrial habitats, and slender, laterally compressed snakes are associated with arboreal lifestyles (Pizzatto et al. 2007). In general, *T. pardalis* matches the terrestrial body plan, *T. semicinctus* matches the arboreal body plan, and *T. melanurus* lies in between, as it looks robust and laterally compressed (Hedges 2002; Rodríguez-Cabrera et al. 2016, 2020a, 2021a, 2021b). Structural habitat partitioning remains formally untested in this assemblage, but anecdotal observations strongly suggest they do segregate spatially, which would explain coexistence despite the high overlap in diet of some categories. Because snakes must utilize their habitats to find food, trophic and spatial niche axes are often highly as-

sociated (see Reinert 1993 for a review). Nonetheless, in some snake communities, trophic niche partitioning is not as evident as habitat partitioning (see Luiselli 2006 for a review). Some European vipers (genus *Vipera* Garsault, 1764) show a high overlap in their diets but segregate by habitat (see Luiselli 2006 for a review). Different foraging strategies have also been documented in North American colubrids (e.g., Fitch 1982, 1999; Lind and Welsh 1994; Luiselli 2006). *Tropidophis pardalis* has been regarded as a ground-dwelling species, which possibly captures its prey at the ground level. In contrast, *T. semicinctus* is a semi-arboreal species that seems to employ an active foraging strategy to find sleeping anoles in the vegetation. The authors have observed no fewer than one hundred instances of *T. semicinctus* actively foraging in vegetation more than 2 m above the ground at night. The foraging strategy used by small *T. melanurus* is not clear, as they seem to be morphologically intermediate between terrestrial and semi-arboreal *Tropidophis*. Small *T. melanurus* have been repeatedly observed actively foraging both on the ground and in vegetation, most often at night (Hernández Dauval and Fundora Caballero 2022). In any case, additional studies on habitat use and activity time of these three species are needed to arrive at conclusions regarding segregation along axes other than the trophic niche.

Anolis sagrei, the prey species most frequently consumed by *T. semicinctus*, *T. pardalis*, and small *T. melanurus* (Table 1), is a generalist lizard that occurs from under rocks and on low grasses to above 2 m high on bushes and trees. This wide use of the spatial niche axis by *A. sagrei* also occurs at night regarding sleeping perch sites. This would provide opportunities for spatial niche segregation among these three snake categories.

Despite the slender body and climbing habits of some Cuban *Tropidophis*, they have been regarded as semi-arboreal because they do not show the high degree of specialization of truly arboreal snakes that spend most of their lives in trees. Cuban *Tropidophis* seem to strongly depend on ground-level shelter when escaping disturbances; our target species even share resting sites (Rodríguez-Cabrera et al. 2022; Torres et al. 2024). Because several individuals of *T. semicinctus* have been observed active on or near the ground at night, it is possible that they also forage at this level, particularly in open areas with sparse shrub-like vegetation where the species occurs in the study area. This would at least partially explain the high dietary overlap between this species and its two congenerics analyzed: *T. pardalis* and small *T. melanurus*. Coexistence under high dietary and habitat overlap could also be explained by a high abundance of the shared resources. For example, both *A. ophiolepis* and *A. sagrei* can be very abundant locally.

The three snake species analyzed, including the two size classes of *T. melanurus*, showed a narrow Levins' niche index ($B' < 0.3$), suggesting a high degree of trophic specialization. All of them consumed only a few prey types in higher proportion (Table 1). The two smaller species, as well as small *T. melanurus*, appear to have diets specialized in anoles. However, at least *T. pardalis* is also known to prey upon frogs of the genus *Eleutherodactylus* and introduced geckos (Armas and Iturriaga 2017; Rodríguez-Cabrera et al. 2020a, 2020b; Rodríguez-Cabrera and Hernández Gómez 2021). It is likely that these alternative prey types are also consumed in the study area, albeit at lower frequencies than anoles. While *Eleutherodactylus* and anoles were the most frequently encountered small vertebrates in the study area, other potential prey types – such as other lizard genera, toads, and murid rodents – occur in the area (Borroto-Páez 2009; Rodríguez Schettino et al. 2013; Rivalta González et al. 2014; Torres López et al. 2017), but were not detected in the diet, possibly due to lower availability, selectivity by the snakes, or limitations of our sampling. Large *T. melanurus* can consume a variety of prey items, including birds and mammals. However, the fact that amphibians accounted for 95% of the diet of large *T. melanurus* strongly suggests that this species specializes in this prey type, at least as adults (Fig. 3). These results are consistent with previous dietary records for the species (Rodríguez-Cabrera et al. 2020a, 2021b).

The relatively large size of this species makes possible the use of different trophic resources across the snake's developmental stages. Our results support a marked ontogenetic dietary shift in *T. melanurus*, with juveniles specializing in anoles before switching to amphibians. Though the sample size for small individuals is limited, larger adults (> 600 mm TL) have a broader diet since they also consume toads and endotherms. Notably, individuals around 350 mm TL may already consume endotherms, as supported by the authors' ex situ observations of specimens accepting mice and House Sparrow (*Passer domesticus*), and a 480 mm specimen containing a Yellow-faced Grassquit (*Tiaris olivacea*) in its stomach (Rodríguez-Cabrera et al. 2017, 2021b). In contrast, we do not expect such a pronounced ontogenetic dietary shift in *T. semicinctus* or *T. pardalis*, as the difference in body size between juveniles and adults is apparently less marked (authors, pers. obs.), likely limiting their ability to handle significantly larger prey as they grow. Nonetheless, this hypothesis remains to be tested.

Trophic niche partitioning in Cuban *Tropidophis* likely depends on multiple factors beyond those explored here, including habitat, distribution, seasonality, and more. Due to their elusive nature, collecting large datasets is challenging. However, species like *T. melanurus*, with higher densities, offer opportunities for more detailed ecological studies. Continued research is essential to understand *Tropidophis* assemblages and their ecological roles in Cuba.

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Appendix 1

Sampled localities within the study area. The consecutive numbers coincide with those in Fig. 1. Datum for all coordinates (North, East) is WGS 84. At least one individual of each of the three species studied was observed in all localities.

Cuba: Villa Clara province: Manicaragua municipality: Gómez village (22.3217, -79.9612). Ranchuelo municipality: North of the Palmarito dam (22.3673, -80.0324). Santa Clara municipality: Quemado de Hilario (22.3841, –80.0209); between the Virginia and José Martí neighborhoods (22.4058, –79.9955); Virginia neighborhood (22.4076, –79.9855); Yabú (22.4679, –79.9887); downtown Santa Clara city (22.4056, –79.9653); "Arcoiris" recreational center (22.4010, –79.9258); Sabanas de Santa Clara Protected Area (22.4015, –79.9140); Loma La Carrera, east of Callejón de los Patos village (22.4327, –79.8572); north of La Minerva Dam (22.4356, –79.8059). Cifuentes municipality: southeast of San Miguel (San Gil) village (22.5016, –79.8803).